

DIEL ACTIVITY RHYTHMS AND THERMOREGULATORY BEHAVIOR OF BLUEGILL IN RESPONSE TO UNNATURAL PHOTOPERIODS

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In reviews of Webb and Brown (1959), Cloudsley-Thompson (1961), Harker (1964), and Bübbing (1967), it is apparent that among vertebrates, rhythms of birds and small mammals have received the greatest research attention.

Scattered reports, however, confirm the existence of daily periodicities in feedings and movements of several fish species in nature and under laboratory conditions [see Schwassmann (1971) and Beitinger (1974a) for references]. The majority of the observed daily periodicities of fishes appear to be cued by cyclic variations in light intensity and related to feeding behavior. However, extensive work by Barlow (1958) indicates that temperature is the critical stimulus in cyclic movements of the desert pupfish, *Cyprinodon macularis*.

Experiments (Beitinger, Magnuson, Neill and Shaffer, 1975) with green sunfish, *Lepomis cyanellus*, revealed the presence of a diel pattern in tunnel-pass frequency (i.e., locomotor activity) of fish in our temperature-preference apparatus. Although simulated natural diel changes in day length directly affected locomotory activity, they did not significantly influence diel or hourly thermoregulatory performance of green sunfish.

In the following experiments two potentially disruptive, unnatural photoperiods were imposed to (1) determine the relationship between photoperiod and diel activity patterns, and (2) test the stability of thermoregulatory behavior of bluegill, *Lepomis macrochirus*. In particular, I looked for evidence suggesting the presence or absence of an endogenous component mediating activity patterns of thermoregulating bluegill.

MATERIALS AND METHODS

Apparatus

The test apparatus is described in detail by Beitinger (1974a) and Beitinger *et al.* (1975). The design (Neill, Magnuson and Chipman, 1972) substitutes a temporal temperature gradient for the spatial gradient typical of most preferred-temperature studies and allows an individual fish to control its thermal exposure. Each 50-liter test tank is divided into halves with a molded fiberglass partition. A tunnel in the partition allows the fish to choose between halves differing by a fixed 2° C temperature interval. Movements through the tunnel are monitored by a pair of photoelectric cells. Passage of a fish into the warmer tank half causes the temperature of the *entire* tank to increase at a constant rate of 3° C/hr, while maintaining the constant 2° C differential between tank halves. When a fish

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swims into the cooler half of the tank, the temperature decreases at the same rate (3°C/hr) in both tank halves until the fish again moves to the warmer tank half. By moving back and forth in this manner, a fish is able to control the minimum and maximum temperatures to which it is exposed. For this study a potential temperature range of 4°C to 55°C was available.

Illumination was provided by an incandescent bulb positioned above the center of each test tank. Bulbs were wired in parallel to a 24-hr timer joined to a capacitor-dimmer circuit. The latter provided a "soft on/soft off" light regime to simulate variations in light intensity which occur during dawn and dusk. Light intensity varied from about 1 footcandle during full illumination to 0 footcandles at full darkness.

Temperatures of each tank half were continuously monitored by a thermistor-wheatstone bridge circuit connected to a multi-channel analog recorder. Upper avoidance temperatures recorded as local maxima were computed from temperature records of the warmer half of each tank, while lower avoidance temperatures recorded as local minima were computed from temperature records of the cooler tank half. A local maximum was designated as an upper avoidance temperature if immediately preceded and followed by an interval when the warmer tank half was at least 0.5°C lower than the local maximum. Similarly, a local minimum was tallied as a lower avoidance temperature if preceded and followed by an interval when the temperature of the cooler tank half was at least 0.5°C higher than the local minimum. A mathematical description of avoidance (turn-around) temperatures was presented by Neill, Magnuson and Chipman (1972). The preferred temperature of each fish was operationally defined as the temperature midway between the two avoidance temperatures. Throughout the experiment, the number of passes through the tunnel by each fish, tallied by an event recorder, were utilized as a measure of fish locomotor activity.

Procedures

One fish was introduced per tank and allowed to experience the static system for 2.5 days with tank halves set 1.0°C above and 1.0°C below the fish's thermal acclimation state. The test period then began and tank temperature control was relinquished to each fish. Data collected during the first 24 hours were not analyzed. Two separate experiments were conducted.

In the first, bluegill, 87 ± 7.8 mm total length, captured during spring from Lake Wingra (Dane County, Wisconsin) were acclimated to 25°C and a LD 12:12 (*i.e.*, light/dark) photoperiod for 4 weeks. Nine fish were placed in the preference aquaria. Temperature and activity records collected during the second, third and fourth test days constituted control data. Following completion of the fourth day, photoperiod was switched from LD 12:12 to LD 6:6:6:6 and data were collected for an additional 72 hours.

Procedures in the second experiment were similar to the first, except bluegill (78 ± 6.2 mm total length), captured during summer from Lake Wingra, were initially acclimated to a LD 15:9 photoperiod and 25°C for 4 weeks. Following the 4-day control period (LD 15:9), a constant light regime (LL) was imposed on test fish and data were collected for an additional 96 hours. In both experiments, fish were fed pellets once each 24 hours on a random schedule during

TABLE I

Thermoregulatory performance of individual bluegill under control (LD 12:12) and experimental (LD 6:6:6:6) photoperiods. All values are temperatures in °C (sd equals standard deviation; grand mean equals the mean of the 7 individual means).

Fish	LD 12:12					LD 6:6:6:6				
	Avoidance temperatures				Preferred temperature	Avoidance temperatures				Preferred temperature
	Lower		Upper			Lower		Upper		
	Mean	sd	Mean	sd	Mean	sd	Mean	sd		
1	29.8	0.9	33.6	1.0	31.7	29.0	0.9	33.2	0.7	31.1
2	29.6	0.4	33.0	0.4	31.3	29.8	0.5	33.3	0.6	31.6
3	28.6	0.6	32.3	0.6	30.4	28.4	0.6	32.3	0.5	30.4
4	29.0	0.7	33.4	1.0	31.2	28.3	0.7	33.0	0.8	30.6
5	29.8	0.5	33.7	0.8	31.8	30.0	0.4	34.0	0.8	32.0
6	28.3	0.6	32.9	0.6	30.6	28.0	0.6	32.6	0.9	30.3
7	28.6	1.0	32.6	0.9	30.6	28.2	0.7	32.6	0.8	30.4
Grand mean	29.1		33.1		31.1	28.8		33.0		30.9

a light period. Pellets were introduced into the tank half occupied by each fish at the moment of feeding.

Locomotor activity and thermoregulatory performance data before and after photoperiod switch were compared. For each fish, the total number of tunnel passes each 0.5 hr (Experiment 1) and 1.0 hr (Experiment 2) was determined. The median for each 0.5 hr or 1.0 hr was plotted to present activity trends throughout both experiments. Also, hourly (or half-hourly) median activity data were pooled into 24-hour cycles for each photoperiod regime.

RESULTS

Temperature regulation

Two of the initial bluegill tested in the first experiment died owing to electronic failure. During the control LD 12:12 photoperiod, the remaining 7 bluegill had grand mean lower and upper avoidance temperatures of 29.1° C and 33.1° C, which yielded a preferred temperature of 31.1° C (Table I). During the two photoperiods, mean performance values of *individual* bluegill differed by 0.2 to 0.8° C (lower avoidance), 0.0 to 0.6° C (upper avoidance) and 0.0 to 0.6° C (preferred temperature). However, statistical comparisons of grouped differences yielded no significant trends in direction or magnitude for any of these thermoregulatory performance parameters (Wilcoxon matched pairs, signed ranks, all $P > 0.05$).

Thermoregulatory precision, reflected by the standard deviation of individual mean avoidance temperatures, also was not significantly influenced by the imposition of LD 6:6:6:6 photoperiod.

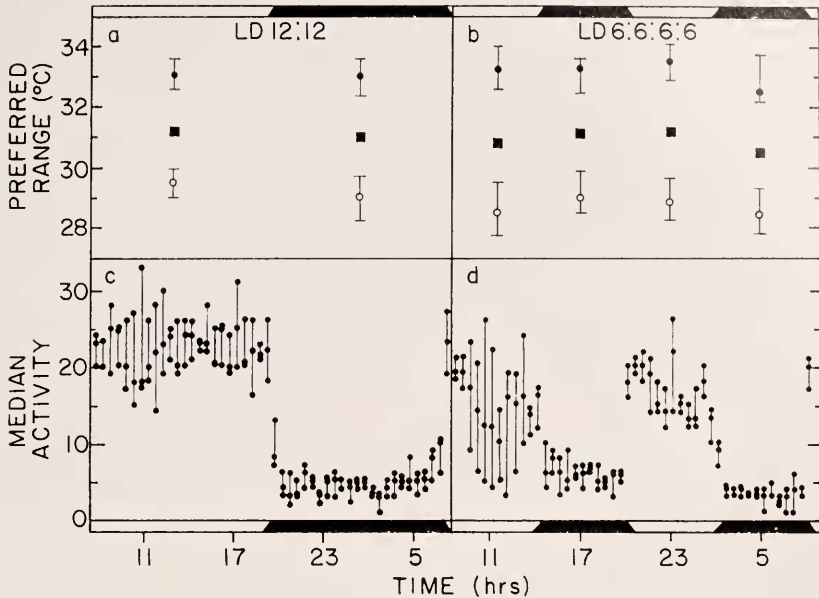


FIGURE 1. Thermoregulatory performance and locomotor activity of bluegill exposed to photoperiods of LD 12:12 and LD 6:6:6:6. Data collected during each photoperiod were pooled into their respective 24 hour cycles. Panels a and b show first and third quartiles and median lower (open circle) and upper (closed circle) avoidance temperatures calculated from data collection during each light and dark interval of both photoperiods. Preferred temperatures are represented by closed squares. Panels c and d present pooled median 0.5-hourly activity levels of the same fish.

Figure 1 (a and b) presents the preferred temperature range for each of the six light and dark intervals during this experiment. All individual avoidance temperatures generated during the six test days were pooled by the time of their occurrence into appropriate light or dark intervals. Then, median and interquartile lower and upper avoidance temperatures were determined and plotted for each light and dark interval. Preferred temperatures (represented by enclosed squares) ranged from 30.5° C to 31.2° C. Utilizing the two limits of the interquartile range (25th and 75th percentiles) and median (50th percentile) as representative data from each interval, a Kruskal-Wallis, one-way analysis of variance was performed. Results confirmed that neither the lower ($P = 0.43$) nor the upper ($P = 0.53$) avoidance temperatures varied significantly among the six intervals. The observed increase in variability of LD 6:6:6:6 data is partly attributable to differences in experimental time, *i.e.*, each interval in LD 6:6:6:6 encompassed only 15 total hours (with 1 hr twilight excluded, 5 hrs \times 3 days = 15 hours for each of the light and dark intervals), whereas each of the two LD 12:12 intervals were of 33 hours duration (again, with exclusion of twilight, 11 hr \times 3 days = 33 total hours). This resulted in large differences (N ranged from 16 to 112) in the number of avoidance temperatures generated by fish during the various light and dark intervals.

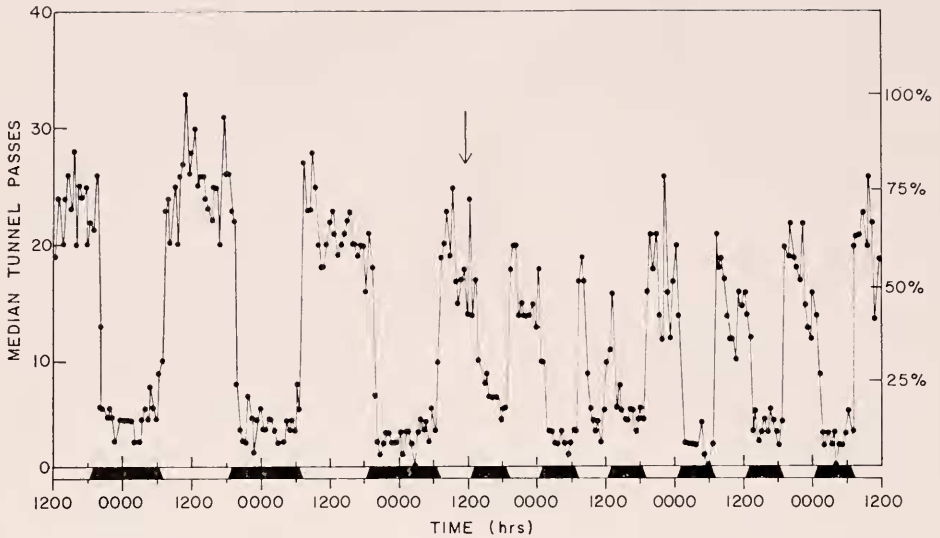


FIGURE 2. Median activity (0.5-hour, tunnel pass frequency) of 7 bluegill during the six day experiment. The arrow indicates when photoperiod was switched from LD 12:12 to LD 6:6:6:6.

Activity patterns

During the LD 12:12 (control) period, a distinct diurnal activity pattern was apparent (Figures 1c and 2). Day and night median activity levels (tunnel passes 0.5 hr) ranged between 15–33 and 1–10, respectively, and were highly significantly different ($P < 0.01$, Mann-Whitney U test). Fish demonstrated no obvious anticipation of dawn or dusk (Figure 1c). Activity levels varied sharply with illumination changes: activities increased during dawn and decreased following dusk.

To facilitate discussion of the LD 6:6:6:6 experimental period, the following time intervals were operationally defined: (1) abnormal dark—dark period from 1400–1900 hr; (2) normal dark—dark period from 0200–0700 hr; (3) abnormal light—light period from 2000–0100 hr; and (4) normal light—light period from 0800–1300 hr. Data collected during the hours when illumination intensity changed (*i.e.*, dawn and dusk) were omitted from analyses. In intervals 1 and 3 above, illumination levels were out-of-phase with the previous light/dark cycle; hence, responses during these intervals are of particular interest.

Activities of fish during the first abnormal dark period did not follow the typical “dusk response” in which activity decreases sharply with decreases in illumination (Figure 2). Median 0.5-hourly activity of fish during the first two out-of-phase dark intervals was increased significantly when compared to the activities of their successive in-phase dark intervals or any of the three LD 12:12 nights (Mann-Whitney U, $P < 0.01$). By the third 24-hour period of LD 6:6:6:6, however, in- and out-of-phase dark activities were no longer different (Mann-Whitney U, $P > 0.05$).

TABLE II

Thermoregulatory performance of individual bluegill under control (LD 15:9) and constant light (LL) photoperiods. All values are temperatures in °C (sd equals standard deviation; grand mean is the mean of the 8 individual fish means).

Fish	LD 15:9					LL				
	Avoidance temperatures				Preferred temperature	Avoidance temperatures				Preferred temperature
	Lower		Upper			Lower		Upper		
	Mean	sd	Mean	sd		Mean	sd	Mean	sd	
1	28.8	0.6	32.8	0.5	30.8	29.0	0.6	32.9	0.6	31.0
2	28.8	1.4	32.3	1.4	30.6	28.8	1.7	31.3	2.0	30.1
3	31.6	0.5	34.8	0.7	33.2	33.1	1.0	35.8	0.9	34.4
4	26.5	1.6	30.5	1.6	28.5	26.6	2.0	31.0	2.0	28.8
5	31.4	0.9	35.3	1.3	33.3	31.0	0.7	34.4	0.7	32.7
6	30.6	1.0	33.1	0.8	31.9	30.8	1.0	33.4	0.8	32.1
7	31.0	0.5	33.6	0.6	32.3	30.4	0.3	33.3	0.5	31.9
8	29.4	0.6	31.7	0.7	30.6	29.6	1.2	31.7	1.2	30.7
Grand mean	29.8		33.0		31.4	29.9		33.0		31.4

Comparing successive normal and abnormal light intervals, only in the first 24-hr period were activities significantly different (Mann-Whitney U, $P = 0.002$). Although a sharp increase in activity appeared when illumination levels increased, the sharp decrease in activity as illumination decreased was not apparent (Figure 1d).

Although significant differences were observed in activity levels of bluegill during light and dark intervals, there was no correlation between activity levels and avoidance temperatures (Spearman rank correlation, $r_s = 0.16$). Thermoregulatory performance of bluegill remained relatively constant.

Temperature regulation

During LD 15:9 photoperiod of the second experiment, the 8 surviving bluegill had grand mean lower and upper avoidance temperatures of 29.8° C and 33.1° C, and preferred temperature of 31.4° C. Switch to constant light conditions (LL) did not influence thermoregulatory behavior, as all three mean performance parameters were within 0.2° C of their respective control values (Table II). There were no significant trends in direction or magnitude of either avoidance temperatures or preferred temperature during LL when compared to those during LD 15:9 (Wilcoxon, all $P > 0.05$).

Although performance data for fish were more variable in Experiment 2, individual preferred temperatures during the four separate photoperiods of the two experiments were not significantly different (Kruskal-Wallis, one-way, analysis of variance, $0.70 > P > 0.50$).

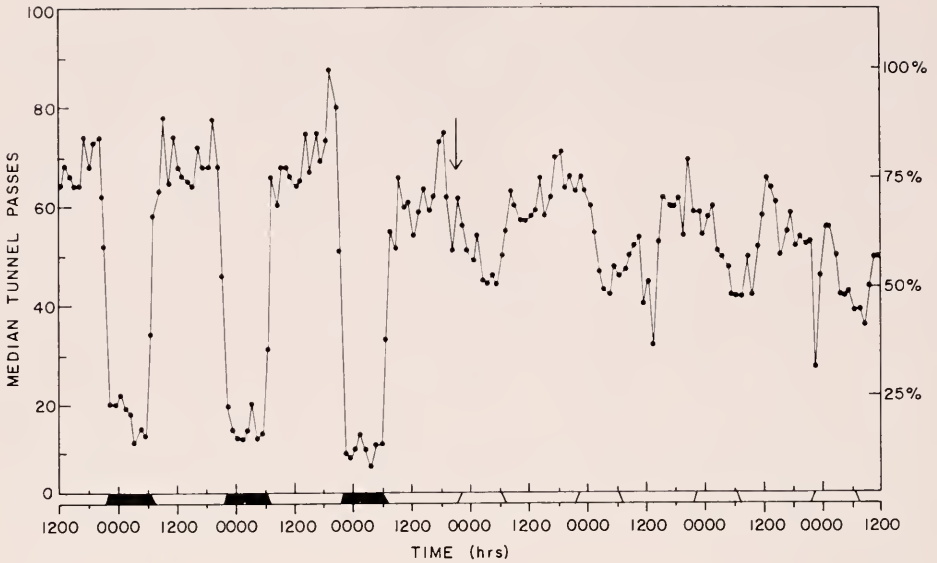


FIGURE 3. Median hourly activity of 8 bluegill exposed to a LD 15:9 photoperiod for three days and constant light for 4 days. The spaces between pairs of diagonal lines in the abscissa indicate when darkness would have occurred under the LD 15:9 photoperiod regime.

Activity patterns

The influence of simulated diel changes in light intensity on bluegill activity is well illustrated in Figure 4, formulated from pooled LD 15:9 activity data shown in Figure 3. Fish were highly active during the lighted portions, moderately active during the crepuscular times and least active during dark. Following switch to LL, the striking diurnal activity pattern observed under LD 15:9 was no longer apparent (Figure 3). During LL, day-time activity levels were lower and "night-time" activities were higher than those during corresponding times in LD 15:9.

A one sample run test (Siegel, 1956) indicated that the order of the 96 hourly activity medians during LL was not random, *i.e.*, a pattern existed ($Z = 6.78$, $P < 0.001$). Then periodogram analysis (Enright, 1965a, b) was applied to LL activity data. The resultant periodogram (Figure 5) has a broad spectral peak with a maximum amplitude between 24.5 to 25.0 hours, as well as an axis of symmetry near this time range. Although this analysis does not prove the existence of a circadian rhythmicity especially when applied to records of only four days, results suggest that a persistent rhythm was present in this data.

DISCUSSION

Preferred temperatures for bluegill in these experiments are consistent with those reported by Neill and Magnuson (1974) and Beitinger (1974b) using a similar experimental approach. Also, these values are within 1° C of the final temperature preferendum for this species determined in a vertical gradient of tem-

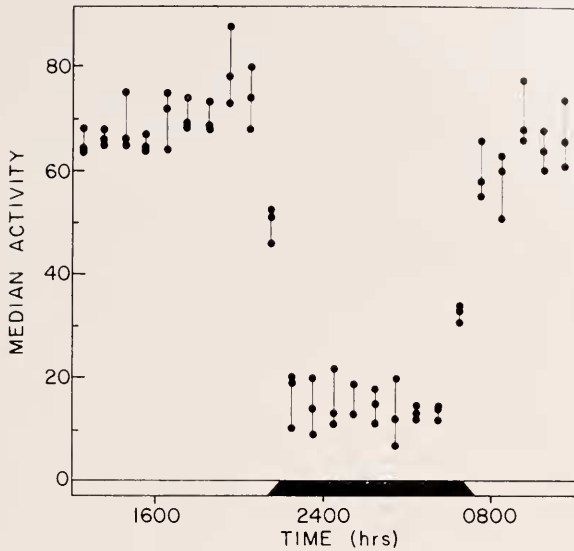


FIGURE 4. Hourly activity data of bluegill under 3 days of LD 15:9 pooled to show 24-hour rhythmicity.

perature by Fry and Pearson (1952). These laboratory-derived preferred temperatures approximate the deep muscle temperature and estimated temperature acclimation state of similar sized bluegill collected during daylight, in summer, from a thermal discharge area of Lake Monona (Neill and Magnuson, 1974).

Thermoregulatory performance of bluegill did not differ greatly between day and night (Figure 1a) or among 6-hour light and dark intervals (Figure 1b). The

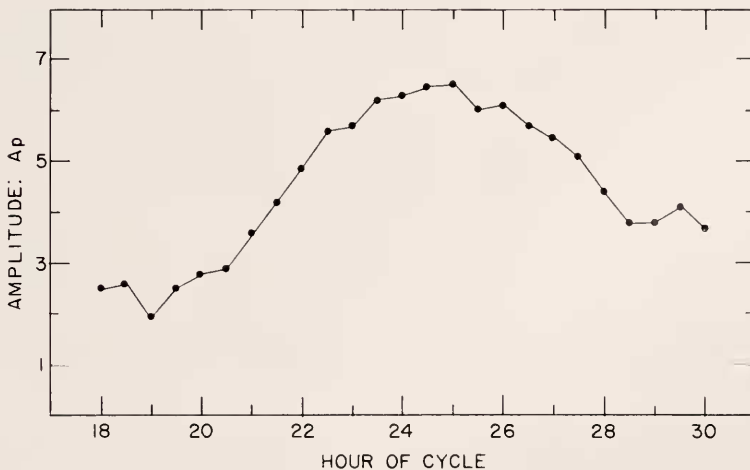


FIGURE 5. Periodogram computed from median hourly activity data of bluegill under 4 days of constant light.

night-time preferred temperature was 0.25°C lower than that during daytime; however, this difference does not approach the 2 to 3°C decrease in body temperature for night-captured bluegill reported by Neill and Magnuson (1974). This inconsistency in night preferred temperatures between laboratory and field data could be due to the intervention of natural non-thermal factors which are either controlled or absent in my laboratory system.

The influence of illumination on temperature selection of fishes has received little research attention. The mosquito fish, *Gambusia affinis*, was observed by Winkler (1973) to thermoregulate behaviorally only during daylight. Sullivan and Fisher (1954) found that temperature selection by brook trout, *Salvelinus fontinalis*, was more precise statistically in dim light (~ 0.15 footcandles) than in bright light (~ 15 footcandles), however, the mean and median preferred temperatures were the same (10.5°C) under both intensities.

The imposition of the two unnatural photoperiod regimes did not disrupt thermoregulatory ability or performance of test bluegill. Preferred temperatures of individual bluegill prior to and following photoperiod switches were similar. Of particular interest is the observation that preferred temperatures of fish under the four separate photoperiods were not significantly different. These findings attest to a stability in thermoregulatory behavior of bluegill.

Whether the relationship between activity and thermoregulation in this experimental design is cause and effect (or effect and cause) is not known. Bluegill during the 2.5 day, temperature-static portion of Experiment 1 were also diurnally active. However, in comparing activity levels, these same bluegill were more than twice as active while thermoregulating. The low correlation ($r_s = 0.16$) between activity and preferred temperatures reveals that activity by bluegill does not exert a primary influence on the temperatures preferred. For a further discussion of the relationship between activity levels and thermoregulatory performance inherent in this experimental design, see Neill (1971) and Beiting, Magnuson, Neill and Shaffer (1975).

In the control phase of both experiments, bluegill activity patterns were markedly diurnal (Figures 2 and 3). Each dawn, a sharp rise occurred in activity levels following a relatively inactive night. The increase in activity was maintained throughout the light period and then decreased rapidly with decreasing illumination during dark. This pattern for bluegill is similar to those of a variety of diurnally active fish species. In contrast to nocturnally active fishes which utilize tactile, chemical or electrical senses for food location, diurnally active species rely predominately on cone vision and typically are visual feeders, actively foraging for and capturing individual prey items.

Analyses of field captured bluegill from Lake Wingra (Baumann and Kitchell, 1974) support these generalizations. The mean stomach content of 75–95 mm bluegill (same size as those studied in these experiments) captured in September, increased almost linearly from a minimum at 0400 to a maximum at 1800. After 1800, mean stomach content decreased rather precipitously. Lake Wingra bluegill did not appear to feed at night. Thus, the periodicity of bluegill feeding in nature corresponds well with the activity pattern found in these experiments. Possibly, the high daytime activities by bluegill in the preference apparatus represent residual exploratory or food search behavior. Similar nocturnal depressions in feeding have been reported in other diurnally active species such as *Clupea harengus*

(Johnson, 1939), *Salmo salar* and *Salvelinus fontinalis* (Hoar, 1942), and *Salmo trutta* (Swift, 1964). Locomotor activity and feeding patterns of fishes are intimately associated and ecologically adaptive. In diurnally active species, decreases in prey abundance or capture efficiency occur simultaneously with inactivity during night, hence, hunger increases. Locomotor activity, which is an important element of feeding behavior, increases with increasing illumination at dawn.

Natural periodicities in daily illumination seem to be adequate in themselves to elicit the diel activity rhythm observed in bluegill; however, manifestations of an internal biological clock appeared in both experiments. In the first experiment, activity of bluegill exhibited resistance to LD 6:6:6:6 photoperiod entrainment, particularly during the first 24 hours (Figure 2). Activity levels during the first abnormal (out-of-phase) dark period were highly significantly increased over those of LD 6:6:6:6 normal (in-phase) and LD 12:12 dark periods. A similar disparity appeared in the relationship between activities during the first two 6-hour light periods. An endogenous component appeared to be reinforcing the responses to light and dark when they were in-phase with the previous light/dark regime and resisting those that were out-of-phase. However, by the third 24-hour period, no significant differences between in- and out-of-phase light or dark activity levels occurred, indicating bluegill had adjusted to LD 6:6:6:6.

The continuation of a bluegill residual activity periodicity in constant light (Experiment 2) provides more evidence to support the existence of an internal timing mechanism. Although the amplitude was dampened (Figure 3), a rhythm was apparent during the entire 96 hours of constant light. These results indicate bluegill possess or are able to develop an internal timing mechanism, synchronized to the external light/dark cycle. This timing mechanism permits the activity rhythm to continue when the external cues are absent for at least 4 days.

Retention of a pre-feeding response (increase in activity) by bluegill held under constant light (Davis and Bardach, 1965) also indicates the presence of an internal timing mechanism in this species. In contrast to a natural circadian rhythm, the pre-feeding activity rhythm is a learned response to a regular daily feeding. The presentation of food resets the timing of the internal clock each 24 hours. Since feeding was random in the LL experiment reported here, the observed activity rhythm was apparently free-running, possibly accounting for its decrease in amplitude with time. The repetitive pre-feeding response in LL (Davis and Bardach, 1965), the resistance of activity levels to immediate photoperiod entrainment and the continuation of a residual activity periodicity in constant light point to the existence of an internal biological clock in bluegill.

Although there have been few reports of persistent longterm activity periodicities of fish, several species have demonstrated evidence of an internal timing mechanism. Tomcod (*Microgadus tomcod*), scup (*Stenotomus vesicolor* = *S. chrysops*), mummichog (*Fundulus heteroclitus*), largemouth bass (*Micropterus salmoides*) and bluegill held under 12 hour periods of bright and dim light acquired a pre-light, pre-feeding activity; also, mummichog established pre-feeding activity under constant illumination (Davis and Bardach, 1965). Recurrent periodicities in activity after removal of external cyclic stimuli have been reported in goldfish, *Carassius auratus* (Spencer, 1939), ammocoete and adult sea lamprey, *Petromyzon marinus* (Kleerekoper, Taylor and Wilson, 1961), common sole, *Solea vulgaris* (Kruuk, 1963), Atlantic salmon, *Salmo salar* (Ali, 1964), sockeye salmon, *Oncor-*

hynchus nerka (Byrne, 1968), a minnow, *Phoxinus phoxinus* (Müller, 1968), swell shark, *Cephaloscyllium ventriosum* (Nelson and Johnson, 1970), Gymnotid species (Schwassmann, 1971), and Atlantic herring, *Clupea harengus* (Stickney, 1972).

With the exceptions of the swell shark which maintained a circadian activity rhythm for about 18 days under both constant light and darkness and various species of Gymnotidae held under constant darkness, the activity rhythms of none of the above species persisted for more than 5 days after external cues were eliminated. Schwassmann (1971) and Richardson and McCleave (1974) suggest that activity rhythms may not always be good indicators of fish endogenous oscillators. Although more extensive records are required to assess the duration of bluegill activity periodicities in the absence of external light synchronizers, results herein indicate that activity patterns of bluegill in my thermoregulation apparatus are photoperiod entrainable and persist for at least 4 days under constant light conditions.

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SUMMARY

Locomotor activity patterns and temperature regulation of bluegill, acclimated to 25° C and 12-hour light/12-hour dark (LD 12:12) or LD 15:9 were examined prior to and following shifts to unnatural photoperiods. During the control phase of both experiments activity patterns of fish were typically diurnal. Activity levels varied sharply with changes in illumination intensity: activity increased during dawn and decreased following dusk. When photoperiod was switched to LD 6:6:6:6 (from LD 12:12) fish activity levels indicated a resistance to photoperiod entrainment, particularly during the first 24 hours. Following switch from LD 15:9 to constant light (LL), the striking diurnal pattern of activity observed under LD 15:9, was no longer apparent. However, a rhythm persisted throughout the entire 96 hours of LL. Results of both experiments suggest the presence of an endogenous component mediating bluegill diel activity patterns.

Switches to unnatural photoperiods were not disruptive to thermoregulatory behavior of bluegill in either experiment. Performance data collected before and after photoperiod switch in each experiment were similar. Mean preferred temperatures of grouped fish under the 4 different photoperiods (LD 12:12, LD 6:6:6:6, LD 15:9 and LL) ranged from 30.9 to 31.4° C and were not significantly different.

LITERATURE CITED

- ALI, M. A., 1964. Diurnal rhythms in the rates of oxygen consumption, locomotor and feeding activity of yearling Atlantic salmon (*Salmo salar*) under various light conditions. *Proc. Indian Acad. Sci. Section B*, **60**: 249-263.
- BARLOW, G. W., 1958. Daily movements of the desert pupfish, *Cyprinodon macularis*, in the shore pools of the Salton Sea, California. *Ecology*, **39**: 580-587.
- BAUMANN, P. C., AND J. F. KITCHELL, 1974. Diel patterns of distribution and feeding of bluegill (*Lepomis macrochirus*) in Lake Wingra, Wisconsin. *Trans. Amer. Fish. Soc.*, **103**: 255-260.
- BEITINGER, T. L., 1974a. Influence of abiotic and biotic factors on the stability of behavioral thermoregulation in fishes, particularly the bluegill. *Ph.D. Thesis, University of Wisconsin (Madison)*, 240 pp.
- BEITINGER, T. L., 1974b. Thermoregulatory behavior and diel activity patterns of bluegill, *Lepomis macrochirus*, following thermal shock. *Fish. Bull.*, **72**: 1087-1093.
- BEITINGER, T. L., J. J. MAGNUSON, W. H. NEILL, AND W. R. SHAFFER, 1975. Behavioral thermoregulation and activity patterns in the green sunfish, *Lepomis cyanellus*. *Anim. Behav.*, **23**: 222-229.
- BÜNNING, E., 1967. *The physiological clock*. (2nd Ed.) Springer, Berlin, 167 pp.
- BYRNE, J. E., 1968. The effects of photoperiods and temperature on the daily patterns of locomotor activity in juvenile sockeye salmon (*Oncorhynchus nerka*). *Ph.D. Thesis, University of British Columbia, Vancouver*, 125 pp.
- CLOUDSLEY-THOMPSON, J. R., 1961. *Rhythmic activity in animal physiology and behavior*. Academic Press, New York, 236 pp.
- DAVIS, R. E., AND J. E. BARDACH, 1965. Time-coordinated pre-feeding activity in fish. *Anim. Behav.*, **13**: 154-162.
- ENRIGHT, J. T., 1965a. Accurate geophysical rhythms and frequency analysis. Pages 31-42 in Jürgen Aschoff, Ed., *Circadian clocks*. North-Holland Publishing, Amsterdam.
- ENRIGHT, J. T., 1965b. The search for rhythmicity in biological time series. *J. Theoret. Biol.*, **8**: 426-468.
- FRY, F. E. J., AND B. E. PEARSON, 1952. Some temperature relations of the pumpkinseed and bluegill sunfish. *Pub. Ont. Fish. Res. Lab.*, 10 pp.
- HARKER, J. E., 1964. *The physiology of diurnal rhythms*. Cambridge Univ. Press, London and New York, 114 pp.
- HOAR, W. S., 1942. Diurnal variations in the feeding activities of young salmon and trout. *J. Fish. Res. Bd. Can.*, **6**: 90-101.
- JOHNSON, W. H., 1939. Feeding of the herring. *J. Fish. Res. Bd. Can.*, **4**: 392-395.
- KLEEREKOPER, H., G. TAYLOR, AND R. WILSON, 1961. Diurnal periodicity in the activity of *Petromyzon marinus* and the effects of chemical stimulation. *Trans. Amer. Fish. Soc.*, **90**: 73-78.
- KRUUK, H., 1963. Diurnal periodicity in the activity of the common sole, *Solca vulgaris*. *Neth. J. Sea. Res.*, **2**: 1-28.
- MÜLLER, K., 1968. Freilaufende circadiane Periodik von Ellritzen am Polarkreis. *Naturwissenschaften*, **55**: 140 (not seen, quoted from Schwassmann, 1971).
- NEILL, W. H., 1971. Distributional ecology and behavioral thermoregulation of fishes in relation to heated effluent from a steam-electric power plant (Lake Monona, Wisconsin). *Ph.D. Thesis, University of Wisconsin*, 203 pp.
- NEILL, W. H., AND J. J. MAGNUSON, 1974. Distributional ecology and behavioral thermoregulation of fishes in relation to heated effluents from a power plant at Lake Monona, Wisconsin. *Trans. Amer. Fish. Soc.*, **103**: 663-710.
- NEILL, W. H., J. J. MAGNUSON, AND G. D. CHIPMAN, 1972. Behavioral thermoregulation by fishes: A new experimental approach. *Science*, **176**: 1443-1445.
- NELSON, D. R., AND R. H. JOHNSON, 1970. Diel activity rhythms in the nocturnal bottom-dwelling sharks *Heterodontus francisci* and *Cephaloscyllium ventriosum*. *Copeia*, **1970**: 732-739.
- RICHARDSON, N. E., AND J. D. MCCLEAVE, 1974. Locomotor activity rhythms of juvenile Atlantic salmon (*Salmo salar*) in various light conditions. *Biol. Bull.* **147**: 422-432.

- SCHWASSMANN, H. O., 1971. Biological rhythms. Pages 371-428 in W. S. Hoar and D. J. Randall, Eds., *Fish physiology, Vol. VI. Environmental relations and behavior*. Academic Press, New York.
- SIEGEL, S., 1956. *Nonparametric statistics*. McGraw-Hill, New York, 312 pp.
- SPENCER, W. P., 1939. Diurnal activity rhythms in freshwater fishes. *Ohio J. Sci.*, **39**: 119-132.
- STICKNEY, A. P., 1972. The locomotor activity of juvenile herring (*Clupea harengus harengus* L.) in response to changes in illumination. *Ecology*, **53**: 438-445.
- SULLIVAN, C. M., AND K. C. FISHER, 1954. The effects of light on temperature selection in the speckled trout, *Salvelinus fontinalis*. *Biol. Bull.*, **107**: 278-288.
- SWIFT, D. R., 1964. Activity cycles in the brown trout (*Salmo trutta* L.) 2. Fish artificially fed. *J. Fish. Res. Bd. Can.*, **21**: 133-138.
- WEBB, H. M., AND F. A. BROWN, JR., 1959. Timing long-cycle physiological rhythms. *Physiol. Rev.*, **39**: 127-161.
- WINKLER, P., 1973. The ecology and thermal physiology of *Gambusia affinis* from a hot spring in southern Arizona. *Ph.D. Thesis, University of Arizona*, 152 pp.